THE EXTINCT GENUS *PROCOPTODON* OWEN (MARSUPIALIA: MACROPODIDAE) IN QUEENSLAND

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ABSTRACT

Three species of the macropodid genus *Procoptodon* Owen are recognised in the Upper Cainozoic deposits of Queensland. Of these, *P. goliah* and *P. rapha* are less commonly encountered than the smaller *P. pusio*.

The majority of specimens were derived from the Pleistocene fluviatile deposits of the Darling Downs, southeastern Queensland; a single specimen has been recorded from cave and fissure-fill deposits. *Procoptodon* appears to be restricted to Pleistocene deposits in Queensland and elsewhere in Australia. Its morphology suggests successful adaptation to a browsing habit.

The fossil macropodids of the Pleistocene fluviatile deposits of the Darling Downs area, southeastern Queensland, comprise the bulk of the representatives of the family yet recorded from Queensland and constitute a rich and diverse assemblage of grazing and browsing animals. Particularly common among these are species which probably frequented open sclerophyll or open grassland habitats. Although many of the Pleistocene species were bigger than present-day macropodids, the larger browsing species of *Procoptodon* Owen appear to have been dominant in size. The genus is, however, also represented in the deposits by a smaller species. *Procoptodon* is generally less well represented numerically than many of the grazing macropodids. In most cases, however, the samples are sufficiently large to enable some assessment of size and morphological variation.

Several important contributions to an understanding of the taxonomy of species of *Procoptodon* have recently been presented, the most notable being those of Stirton and Marcus (1966) and Tedford (1967). Study of the Queensland representatives of the genus is considered important in indicating the variation present in the type area and in supplementing the studies based on non-topotypic samples. This investigation also provides a basis for comparison with samples known to exist in other Australian Pleistocene deposits.

Stirton and Marcus (1966) have suggested that detailed descriptions might be forthcoming from deposits at Bone Camp Gully, a tributary of Ironbark Creek, 15 miles east of Bingara, north-eastern New South Wales. These deposits contain macropodid species also reported in the fluviatile deposits of the Darling Downs (Bartholomai, 1963). Tedford (1967) has described specimens referred to the type species, *P. goliah* (Owen), from Lake Menindee, western New South Wales.

No specimens of *Procoptodon* have as yet been recovered from the possibly Pliocene Chinchilla Sand, in the western Darling Downs, nor have any been found elsewhere in Australia in deposits believed to be older than Pleistocene.

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Measurements throughout are in millimetres and, unless otherwise specified, all specimens mentioned are held in the collections of the Queensland Museum, Brisbane. Where summaries of measurements are provided, original data are held in the library of the Queensland Museum, Brisbane.

Family MACROPODIDAE
Subfamily MACROPODINAE
Genus **Procoptodon** Owen, 1873

TYPE SPECIES: *Macropus goliah* Owen, 1846, by subsequent designation (Owen, 1874).

GENERIC DIAGNOSIS: Stirton and Marcus (1966) and Tedford (1966) have each presented a generic diagnosis for *Procoptodon* based largely on type specimens known or reasonably presumed to have been derived from the Darling Downs deposits, supplemented by referred specimens from the Bingara and Lake Menindee deposits. The diagnoses generally agree with what is known of the genus in the type area but include some morphological aspects not represented in the available Queensland sample.

DISCUSSION: A full historical discussion of the genus is presented in Stirton and Marcus (1966).

Procoptodon has frequently been included with the genus *Sthenurus* Owen, in a separate subfamily, the Sthenurinae. Because of its general macropodine bilophodont condition and pattern of tooth replacement, Bartholomai (1963) retained *Sthenurus* within the Macropodinae. Similar arguments may be presented for *Procoptodon*, although

this genus appears to be considerably more specialised, not only in its dentition but also possibly in aspects of its postcranial skeletal morphology. Tedford (1967) has shown that in *P. goliah* the pes approaches a monodactylous condition, with even the fifth metatarsal considerably reduced. The forelimb is comparatively more elongate than in most other macropodines. The post-cranial skeleton is not known in other species of *Procoptodon*, and it is considered unlikely that specialisation to this extent would necessarily be true of *Sthenurus* as well. For this reason, the broader classification is here applied and *Procoptodon* is regarded as a highly specialised macropodine.

Procoptodon goliah (Owen, 1846)

(Pl. 16, figs. 1-3; pl. 17, fig. 3; pl. 18, figs. 3-4)

Macropus goliah Owen, 1846, p. 59; Flower, 1884, pp. 720-1.

Procoptodon goliah (Owen): Owen, 1873, pp. 386-7; 1874 (*partim*), pp. 791-7, pl. 79, figs. 1, 8, 10; pl. 80, figs. 1-4; 1877 (*partim*), pp. 460-5, pl. 94, figs. 1, 8, 10; pl. 95, figs. 1-4; Lydekker, 1887 (*partim*), pp. 234-5; 1891, pp. 571-4, pl. 21, figs. 2-2b; Simpson, 1930, p. 78; Stirton and Marcus, 1966, p. 352, figs. 3, 10; Tedford, 1967, pp. 42-84, figs. 9-23.

Procoptodon goliath Etheridge Jun., 1878, p. 190.

[non] *Procoptodon goliah* (Owen): McCoy, 1879, pp. 9-11, pls. 52-3 (= ?*P. rapha* Owen).

Sthenurus goliah (Owen): De Vis, 1895 (*partim*), pp. 89-93, pl. 15, figs. 5-9.

Sthenurus (*Procoptodon*) *goliah* (Owen): Tate, 1948, p. 338.

MATERIAL: F3862, cast of holotype, B.M.(N.H.) No. M1896, partial right maxilla with M^1-M^3, Darling Downs, southeastern Queensland (figd. Owen, 1874, pl. 79, fig. 1; 1877, pl. 94, fig. 1; Stirton and Marcus, 1966, figs. 3a-b).

F1850, partial right maxilla with P^3-M^2, King Creek, Darling Downs. F1328, partial left maxilla with M^3, King Creek, Darling Downs.

F3861, cast of B.M.(N.H.) No. M1897, partial right mandibular ramus, with M_1-M_4, Darling Downs (figd. Owen, 1874, pl. 80, figs. 1-2; 1877, pl. 95, figs. 1-2). F795, partial right mandibular ramus with M_2-M_4, Darling Downs. F797, partial right mandibular ramus with P_3-M_4, Darling Downs. F801, cast of partial left mandibular ramus with M_3-M_4, locality unknown (figd. Owen, 1874, pl. 79, figs. 8, 10, pl. 80, figs. 3-4; 1877, pl. 94, figs. 8, 10, pl. 95, figs. 3-4). F805, partial right mandibular ramus with P_3-M_4, Clifton, Darling Downs. F4457, partial left mandibular ramus with I_1 broken, P_3-M_4, Darling Downs. F4458, partial right mandibular ramus with M_4, Darling Downs.

SPECIFIC DIAGNOSIS: An adequate diagnosis for the species is presented in Stirton and Marcus (1966).

DISCUSSION: Owen's original description is contained in notes transmitted to and published in Waterhouse (1846). Owen (1846) must thus be regarded as the author of the specific name as has been noted by all subsequent workers, with the exception of Tate (1948), who attributed authorship to Waterhouse.

TABLE 1

MEASUREMENTS FOR *Procoptodon goliah* (OWEN) MAXILLA

Specimen	P^3	M^1	M^2	M^3
F3862, cast of holotype ..	—	17.3 × 17.0	21.5 × 19.6	23.6 × 19.8
F1850	15.8 × 10.9	17.8 × 17.0	20.8 × 19.2	—
F1328	—	—	—	22.6 × —

The original description is somewhat confusing, in suggesting that the holotype contained not three, but only two molar teeth in a fragment of a right maxilla. Combined length of these is stated to be $1\frac{1}{2}$ inches while the breadth is indicated as $7\frac{1}{2}$ lines. These measurements concur with the length of M^1M^2, and the protoloph breadth of M^2 in the British Museum (Natural History) specimen, M1896, figured by Owen (1874, pl. 79, fig. 1). This specimen was regarded as the holotype by Lydekker (1887). The specimen thought to be a right maxilla by Tate (1948) and confused with the holotype, is unquestionably a partial left mandibular ramus. It was figured and correctly determined by Owen (1874, pl. 79, fig. 8).

The molar teeth contained in the holotype maxilla were interpreted by Owen (1874) as M^2–M^4. This determination was questioned by Stirton and Marcus (1966) and was shown by Tedford (1967) to be incorrect. The teeth represented are M^1–M^3. Evidence to support this identification has been gained from a comparison of a cast of the holotype with F1850 a maxillary fragment with P^3 exposed by fenestration and M^1–M^2. The first two molars of the holotype are nearly identical in size and proportion with those in F1850, as seen in table 1. Further, the teeth are morphologically inseparable, while the jugal processes and anterior limits of the post-palatal vacuities are similarly positioned in both specimens.

Examination of Owen's (1874, 1877) figures indicates that some of the specimens examined by that authority have been incorrectly determined as *P. goliah*. Strong accessory ornamentation, the open nature of the antero-labial metaloph "pocket" on the molars, and near vertical labial and lingual molar crown margins are conspicuous in the specimens depicted by Owen (1874, pl. 79, figs. 2-7, 9), indicating that these are, in fact, of *P. rapha* described below. In the case of the specimens illustrated by Owen (1874, pl. 80, figs. 5-8), diagnostic details cannot be evaluated in the views provided, but these may also be incorrectly associated with *P. goliah*. The P^3 shown in Owen (1874, pl. 80, fig. 7) from the lingual aspect, cannot be duplicated in its morphology in the samples available in the Queensland Museum, but in view of its apparent size, it is believed that this most likely represents extreme variation in *P. rapha* rather than in *P. goliah*. Considerably greater morphological affinity with *P. rapha* is shown in the specimen illustrated by Owen (1877, pl. 92, figs. 1-5), while the illustration presented in Owen (1874, pl. 79, fig. 11) is composite.

TABLE 2

MEASUREMENTS FOR *Procoptodon goliah* (OWEN) MANDIBLE

Specimen	P_3	M_1	M_2	M_3	M_4	Mandible depth and breadth below M_2-M_3
F3861, cast of B.M. (N.H.) No. M1897	—	18.5 × —	22.7 × —	25.1 × —	25.8 × 18.5	40.6 × 33.0
F795	—	—	22.3 × 16.4	24.6 × 18.2	25.7 × 18.3	51.7 × 35.2
F797	12.7 × 9.7	18.0 × 13.0	21.3 × 15.9	23.8 × 17.3	24.5 × 17.3	44.0 × 35.1
F801, cast of specimen figd. Owen (1874, pl. 80, figs. 3-4) ..	—	—	—	24.4 × 18.5	26.5 × 18.6	—
F805	13.5 × 9.5	18.3 × —	21.8 × 15.6	23.5 × 16.5	—	40.3 × 32.5
F4457	13.6 × 11.2	—	—	23.9 × —	25.6 × —	—
F4458	—	—	—	—	— × 21.1	—

Associated upper and lower jaw fragments of *P. goliah* have been recorded from the Lake Menindee area by Tedford (1967), but to date the Queensland deposits have yielded only dissassociated fragments. Morphological similarity of mandibular and maxillary teeth, particularly molars, suggests the correct assignment of mandibular specimens from the type area, and this is verified by comparison with Tedford's (1967) illustrations.

In addition to associated cranial remains, Tedford (1967) also records associated post-cranial material of *P. goliah*, showing marked differences from the post-cranial skeleton in other known macropodids. In particular, the species trends towards a monodactylous condition of the hind foot, with the fifth metatarsal reduced to a mere vestige. The forelimb is comparatively longer than is normal for the family.

Compared with the cast of the holotype, the molars in F1850 and F1328 possess identical convergence of the lateral surfaces of the lophs. In all the angle is 34°. F1328 presents some morphological dissimilarity in lacking an antero-labial metaloph fossette; this character has been considered specifically important by Stirton and Marcus (1966).

Morphologically, the known permanent cheek teeth appear very similar to those preserved in the partial left maxilla, Australian Museum No. MF890, from Bingara, figured by Stirton and Marcus (1966, figs. 4a–b), but the lateral slopes of the molar lophs converge ventrally at 43°. The author considers this variation in the angle of convergence to be intraspecific.

Tedford (1967) figured specimens of *P. goliah* from Lake Menindee almost identical with the Queensland material, but did not provide any assessment of the lateral loph surface convergence present. F799 from the Darling Downs referred to *P. goliah* by Tedford (1967, table 27) is of *P. rapha*.

Lower dentitions figured in Stirton and Marcus (1966) and in Tedford (1967) appear to be morphologically very similar to those in the Darling Downs material. However, no measurements are provided for the angle of convergence of the lateral lophid surfaces of the molars so that no direct comparison is possible in this feature. Convergence in posterior molars in the Queensland sample ranges from 23°–41° ($\bar{X}$=33°; n=6). Some differences in size are evident between this material, measurements for which are provided in table 2, and the Lake Menindee sample, but as these are comparatively minor, no great significance is placed on them.

All specimens in the Queensland Museum, here referred to *P. goliah* have been derived either from the eastern Darling Downs deposits, or have preservation suggesting this area as their likely provenance.

Tedford (1967) has discussed the recorded geographical distribution of *P. goliah* and has indicated its relative paucity in collections. *P. goliah* is recorded definitely from Bingara, Tocumwal and Lake Menindee in New South Wales, possibly from the Pleistocene Malkuni Fauna of the Lake Eyre Basin, and from Calca Station, County Robinson, western Eyre Peninsula, South Australia (Merrilees and Ride, 1965).

Procoptodon rapha Owen, 1874

(Pl. 16, figs. 4-5; pl. 17, fig. 1; pl. 19, figs. 1-3; pl. 20, figs. 1-3)

Procoptodon rapha Owen, 1873, pp. 386-7 (*nomen nudum*).

Procoptodon rapha Owen, 1874, pp. 788-91, pl, 77, figs. 8-12; pl. 78, figs. 1-3; 1877, pp. 457-60, pl. 90, figs. 8-12; pl. 92, figs. 1-5; pl. 93, figs. 1-3; pl. 128, figs. 1-4; Lydekker, 1887 (*partim*), pp. 235-6; 1891, pp. 571-4, pl. 21, fig. 1; Simpson, 1930, p. 75; Stirton and Marcus, 1966, pp. 352-3, figs. 2, 5, 9.

Procoptodon goliah (Owen): Owen, 1874 (*partim*), pp. 791-7, pl. 79, figs. 2-7, 9; 1877 (*partim*), pp. 460-5, pl. 94, figs. 2-7, 9.

(?) *Procoptodon goliah* (Owen): McCoy, 1879, pp. 9-11, pls. 52-3.

Macropus rapha (Owen): Flower, 1884, p. 721.

Sthenurus goliah (Owen): De Vis, 1895 (*partim*), pp. 89-93.

[non] *Procoptodon rapha* Owen: Scott, 1906, 2 pp.

MATERIAL: F3864, cast of holotype, B.M.(N.H.) No. 32885, partial left mandibular ramus with I_1 broken, P_2 and DP_3 excavated from its crypt, Condamine River, Darling Downs (figd. Owen, 1874, pl. 77, figs. 8-12; 1877, pl. 90, figs. 8-12; Stirton and Marcus, 1966, figs. 5a-c).

F782, partial mandibular rami with left P_3–M_4, right P_3, M_3–M_4, Freestone Creek, Darling Downs. F794, partial mandibular rami with left P_3–M_4, right P_3–M_4, Darling Downs. F796, partial left mandibular

ramus with M_2–M_4, Darling Downs. F798, partial left mandibular ramus with M_2–M_4, Darling Downs. F803, partial right mandibular ramus with M_1–M_4, Darling Downs. F804, cast of partial right mandibular ramus with M_1–M_4, locality unknown (figd. Owen, 1874, pl. 78, figs. 1–3; 1877, pl. 93, figs. 1–3). F809, partial right mandibular ramus with M_1–M_2, P_3 exposed from above, Darling Downs. F2430, partial left mandibular ramus with M_2–M_3, King Creek, near Nobby, Darling Downs. F2626, partial left mandibular ramus with M_3–M_4, near Glengallan Creek, 7 miles north of Warwick, Darling Downs. F2636, partial left mandibular ramus with P_3–M_3, Little Middle Creek, Cowabbie, Maidenwell, Darling Downs. F4463, partial right mandibular ramus with M_2, Darling Downs. F4460, partial left mandibular ramus with P_2–M_3, P_3 exposed by fenestration, King Creek, at M.R. 039454 Clifton 1 mile sheet, Darling Downs. F4462, partial left mandibular ramus with M_3, King Creek at M.R. 039454 Clifton 1 mile sheet. F4461, partial right mandibular ramus with M_3, Jimbour Creek, 2 miles south of Jimbour, Darling Downs.

F799, partial left maxilla with M^1–M^3, Darling Downs. F800, partial left maxilla with M^2–M^3, Darling Downs.

SPECIFIC DIAGNOSIS: An adequate diagnosis for this species is presented in Stirton and Marcus (1966).

DESCRIPTION: Mandible large, short, relatively deep, particularly below molar series, with longitudinal axis slightly convex laterally. Symphysis relatively elongate, ankylosed in adult individuals, set at an angle of approximately 40° to base of mandible; produced postero-ventrally resulting in decided ventral extension of basal margin of ramus below P_3–M_1; geniohyal pit very deep, rather high, well anterior to posterior symphysial limit. Diastema short; ventral margin of ramus somewhat acutely rounded between symphysis and diagastric ridge. Mental foramen moderately large, ventral and only slightly anterior to anterior root P_3, near diastemal crest; accessory foramen sometimes present, insignificant, mid-way between posterior root of M_2 and ventral margin of ramus. Ramus with labial groove between mental foramen and anterior root of M_2. Diagastric process postero-ventral of M_4, strongly developed, separated from base of angle by post-diagastric sulcus, bounded above by diagastric fossa; this fossa separated antero-dorsally from extremely shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, leading to post-alveolar ridge, ascending posteriorly on mesial wall of large coronoid process, to above relatively large mandibular foramen. Masseteric crest raised to level of occlusion of cheek teeth, with production of extremely large masseteric foramen; masseteric fossa deep. Anterior margin of coronoid process inclined beyond vertical. Angle and condyle not preserved.

I_1 known only from its broken base.

P_2 small, robust, subtriangular in basal outline, broader posteriorly, shorter than DP_3. Crown with high lingual crest, slightly concave lingually, transected by two sets of vertical ridges between cuspids, with production of cuspules at crest. High, curving labial crest flanked anteriorly by deep, mesial groove. Intervening basin ornamented by ridges from crests.

DP_3 molariform, with hypolophid broader than protolophid; structurally similar to molar series.

P_3 comparatively large, robust, subtriangular in basal outline, broader posteriorly, only slightly shorter than M_1. Crown with high lingual crest very slightly concave lingually, transected between cuspids by three sets of vertical ridges, with production of cuspules at crest. High, curving, labial crest flanked anteriorly by deep, mesial groove. Deep, intervening basin coarsely ornamented by ridges from crests.

$M_1<M_2<M_3=M_4$; molars subrectangular in occlusal view, somewhat constricted across talonid basin; lophids moderately high, slightly convex posteriorly, with lateral lophid surfaces converging only slightly dorsally. Hypolophid slightly broader than protolophid in M_1, approximately equal or slightly narrower in M_2, and narrower in M_3 and M_4. Trigonid basin relatively broad, its length approximately equalling distance between lophids. Forelink high, strong, descending from a point linguad to protoconid, anteriorly to antero-labial margin of relatively high anterior cingulum; high transverse ridge unites with forelink well above cingulum, extending to lingual cingulum limit; weak ridges descend anteriorly from protoconid and metaconid; accessory ridges on anterior surface of protolophid, from forelink and from transverse ridge to anterior cingulum variable, but generally strong; all ridges on molars generally sharply defined. Posterior surface of protolophid variably, but sometimes strongly ridged. Midlink descends postero-lingually from near protoconid, uniting with more extensive antero-labial ridge usually descending from point labiad to mid-point of hypolophid; junction frequently plicate. Accessory ridges from midlink usually transverse, moderately strong, the most anterior frequently limiting a fossette at the antero-lingual midlink extremity; these better developed lingually than labially. Anterior ridges from hypoconid and entoconid poorly developed; very strong ridge descends anteriorly from near midlink into lingual moiety of talonid basin; additional low folds cross talonid, labially and lingually, with development of pits in base of talonid, close to midlink. Variable, but generally strong ridges fron hypoconid, entoconid and from near mid-point of hypolophid descend posteriorly to unite near base of crown; central posterior ridge generally divided basally by groove, while posterior ridge from entoconid nearly always bifid. The strongly developed ridges throughout often secondarily and variably ornamented by very weak ridges.

Upper incisors, P^2, DP^3, P^3 and M^4 not represented.

$M^1<M^2<M^3$; molars subrectangular, slightly constricted across median valley, with lophs moderately high, bowed anteriorly; metaloph broader than protoloph in M^1, approximately equal or slightly narrower in M^2 and narrower in M^3. Lateral loph surfaces converging only slightly ventrally. Anterior cingulum relatively narrow, ascending lingually, short; narrow ridge frequently developed above labial extremity of cingulum, occasionally closed to produce anteriorly directed fossette; numerous, variable, coarse ridges connect

cingulum and anterior surface of protoloph, these becoming stronger towards labial limit, with accessory ridges linguad to variable ridge from paracone frequently extremely well developed. Occasionally, antero-labial fossette developed in association with these ridges. Median valley sharply V-shaped, slightly ascending lingually. Strong midlink ascends from point labiad to mid-point of protoloph, to point linguad to mid-point of metaloph; midlink usually convex labially, ornamented labially and lingually by relatively coarse ridges. Strong ridge ascends posteriorly from near mid-point of protoloph, paralleling midlink and close to it, terminating in median valley. A second strong ridge ascends postero-lingually from paracone, curving lingually to unite with midlink, producing well defined fossette on postero-labial protoloph surface. Subsidiary ridge ascends from this ridge near labial margin, into median valley. Anterior ridge from metacone generally ascends directly into median valley, without production of antero-labial fossette on anterior metaloph surface. Various subsidiary ridges and tubercles are developed between this ridge and midlink. Lingually, surfaces of lophids contributing to median valley usually weakly ornamented, but low, strong, broad ridge crosses valley, delimiting well defined pocket adjacent to midlink. Similar, but weaker pocket developed in corresponding labial moiety position. Posterior metaloph surface with very strong ridge ascending postero-lingually from metacone towards median base of crown uniting with strong posterior ridge from below crest of metaloph linguad to mid-line, and with weaker ridge ascending postero-labially from hypocone. Posterior fossette formed by the two stronger ridges; accessory ridges ascend into posterior fossette. Well developed ridges throughout the molars often secondarily and variably ornamented by very weak accessory ridges.

TABLE 3

SUMMARY OF MEASUREMENTS FOR *Procoptodon rapha* OWEN MANDIBLE

Character	F3864, cast of holotype	n	O.R.	$\bar{X}$	s	V
Length P_2	—	1	—	9.4	—	—
Maximum breadth P_2 ..	—	1	—	7.2	—	—
Length DP_3	—	1	—	12.9	—	—
Breadth protolophid DP_3	—	1	—	9.2	—	—
Length P_3	14.9	8	13.8 — 15.2	14.6	0.6090	4.17
Maximum breadth P_3 ..	10.6	8	9.7 — 10.8	10.4	0.3760	3.62
Length M_1	—	6	16.0 — 18.0	16.8	0.8354	4.97
Breadth protolophid M_1	—	4	11.6 — 12.3	12.0	0.3557	2.96
Length M_2	—	12	18.2 — 20.2	19.1	0.5901	3.09
Breadth protolophid M_2	—	7	13.6 — 15.5	14.4	0.5816	4,04
Length M_3	—	13	20.1 — 23.1	21.5	0.9008	4.19
Breadth protolophid M_3	—	9	14.2 — 16.7	15.1	0.7338	4.86
Length M_4	—	10	20.2 — 23.6	21.5	1.0000	4.65
Breadth protolophid M_4	—	6	13.8 — 15.6	14.6	0.6768	4.64

DISCUSSION: The name *Procoptodon rapha* was introduced by Owen (1873) as a *nomen nudum* but was validly presented the following year (Owen, 1874), accompanied by an adequate description and figures.

The holotype, British Museum (Natural History) number 32885, represents an incomplete mandibular fragment with only P_3 allowing meaningful comparison. This tooth was originally figured within its crypt from the labial and posterior aspects. It was removed and was refigured (Stirton and Marcus 1966, figs. 5a–c). The character of its P_3 is sufficient to distinguish it from *P. goliah*. The separated nature of the labial crest differs markedly from that in *P. goliah*, in which the crest more completely encloses the basin between this and the lingual crest. The tooth is larger and more triangular in occlusal view than in *P. goliah*, the latter feature being consistent in the Queensland sample.

Lydekker (1887) recognised *P. rapha* as a distinct taxon but suggested that its inferior size represented the only means for its separation from *P. goliah* and that because of the size variation evident, it was probable that it would ultimately prove to represent only a small race of the larger species. This suggestion was accepted by De Vis (1895) who placed *P. rapha* in synonymy with *P. goliah*, within the genus *Sthenurus*, a conclusion untenable in the light of current knowledge of the group.

TABLE 4

MEASUREMENTS FOR *Procoptodon rapha* OWEN MAXILLA

Specimen	M^1	M^2	M^3
F799	17.1 × —	20.8 × 18.2	22.0 × —
F800	—	19.5 × 16.2	20.7 × 16.8

Apart fron size differences already noted and the morphological differences between the permanent lower premolars, the species are readily separable by the low angle of convergence of the lateral surfaces of lophs and lophids in upper and lower molars in *P. rapha* as well as by details of the stronger, better developed accessory molar ridging in this form. Mean convergence in *P. rapha* lateral molar lophid and loph surfaces measures 14° in lowers (n=12) and 22° in uppers (n=2). Numerous minor differences are also apparent, as indicated in the revised diagnosis presented in Stirton and Marcus (1966).

The holotype of *P. pusio* was referred to *P. rapha* by Lydekker (1887). These taxa are undoubtedly separate and *P. pusio* is described below. It differs not only in its smaller size but also in its much simpler ornamentation of molar teeth.

Although the material in the collections of the Queensland Museum referred to *P. rapha* is not a statistically large sample, a summary of mandibular measurements is presented in table 3; maxillary measurements are listed in table 4. The size differences between *P. rapha* and *P. goliah* alluded to above can be seen by comparison of these tables with tables 1 and 2. Differences appear greater with respect to the mandibular parameters considered, but this results from the larger sample of mandibular specimens available for examination, and the likelihood of a greater range in observable variation being expressed in these. Lower permanent cheek teeth in *P. rapha* appear to be moderately uniform as evidenced by the relatively low values for the Coefficient of Variation throughout (2.96–4.97). These comform reasonably well with values for V currently known for other fossil species of the Darling Downs deposits (Bartholomai, 1967).

Two specimens present in the Queensland Museum collections show some morphological similarity to *P. rapha* but cannot be referred to the species with certainty. Of these, F4548, a nearly complete right mandibular ramus with M_3–M_4 from Cement Mills, Gore, shows reduced ornamentation of the teeth preserved, although in other respects it is inseparable from *P. rapha*. The Cement Mills cave earths are unstratified cave and fissure-fill deposits, and while these are generally assumed to be of Pleistocene age, they may well contain somewhat younger material. Since *P. rapha* is variable in the accessory ornamentation of its molars, F4548 may well represent only extreme variation in this feature.

The second specimen, F6143, from Jimbour Creek, eastern Darling Downs, a partial left maxilla with M^1–M^2, presents much more reduced ornamentation. Convergence of the lateral molar loph surfaces is in keeping with that in *P. rapha*, but there is almost complete absence of accessory ridging on the antero-labial metaloph surface, on the midlink, and associated with the anterior cingulum, while the strong accessory plate, paralleling the midlink across the antero-lingual portion of the median valley is completely absent. Strong pockets are not formed in the base of the median valley.

All specimens at present referred to *P. rapha* in the Queensland Museum collections have been derived from localities in the fluviatile deposits of the eastern Darling Downs, or have preservation in keeping with their derivation from these deposits.

Stirton and Marcus (1966) figured Australian Museum specimen number MF886, a mandible from the Bingara Fauna, as *P. rapha*. This specimen appears morphologically identical with specimens referred from the eastern Darling Downs and presents the more triangular P_3 typical of the present sample. Lydekker (1891) had previously referred a mandibular specimen from Bingara to the species.

P. rapha is not well recorded elsewhere in Australia. Tedford (1967) suggests that the specimens from Lake Timboon, western Victoria, figured by McCoy (1879) as *P. goliah* may be of *P. rapha*. These specimens present some features which are consistent with the

topotypic sample of *P. rapha*. Measurements for a small sample from Lake Culongulac and Colac in Victoria are presented for comparison in table 5. These indicate a generally slightly larger size than in the Queensland sample, with the exception of P_3 measurements which appear to be well outside the values in the local material. Morphologically, the specimens tend to be slightly less strongly ornamented in their cheek teeth, but are considered to be generally within the range in variation exhibited in specimens of *P. rapha* from Queensland. In view of the size differences seen in the permanent lower premolars, however, it is believed that reference of the specimens to *P. rapha*, at this time, would be premature.

TABLE 5

MEASUREMENTS FOR SOME MANDIBULAR SPECIMENS OF *Procoptodon* IN THE NATIONAL MUSEUM, VICTORIA

Specimen	P_3	M_1	M_2	M_3	M_4	Angle of convergence of lateral lophid surfaces
P26901 + ...	— × 12.0	11.9 × —	20.7 × 14.8	22.0 × 15.9	23.5 × 15.8	14°
P26902 + ...	16.1 × 12.5	17.8 × —	19.5 × 14.0	21.2 × —	22.1 × 14.7	15°
P1909*	—	—	21.2 × —	22.1 × 16.8	22.9 × 16.4	17°

+ from Lake Colongulac, near "Chocolyn", Camperdown, Victoria; * from Colac, Victoria.

The specimen identified as *P. rapha* by Scott (1906) from King Island has been correctly referred to *Sthenurus occidentalis* by Anderson (1932), but the status of the limb fragment from the Mowbray Swamp in Tasmania, recorded by Scott and Lord (1924) as *Procoptodon* cannot be established until more is known of the post-cranial skeleton in smaller species of *Procoptodon*.

Procoptodon pusio Owen, 1874

(Pl. 17, fig. 2; pl. 18, figs. 1-2; pl. 21, figs. 1-3)

Pachysiagon otuel Owen, 1873 (*nomen nudum*), pp. 386-7.

Procoptodon pusio Owen, 1873 (*nomen nudum*), pp. 386-7.

Pachysiagon otuel Owen, 1874, p. 784, pl. 76, figs. 7-10.

Procoptodon pusio Owen, 1874, p. 788, pl. 77, figs. 2-6, 7; 1877, pp. 454-7, pl. 89, figs. 7-10; pl. 90, figs. 2-6, 7; pl. 91, figs. 1-6; Simpson, 1930, p. 75; Stirton and Marcus, 1966, pp. 353-4, figs. 1, 6-8.

Procoptodon rapha Owen: Lydekker, 1887 (*partim*), pp. 235-6.

Procoptodon otuel (Owen): Lydekker, 1887, pp. 236-7; Simpson, 1930, p. 75.

Sthenurus otuel (Owen): De Vis, 1895, pp. 93-4, pl. 16, figs. 1-4.

MATERIAL: F3863, cast of holotype, B.M.(N.H.) specimen 39996, associated partial right and left maxilla with M^1–M^3, P^3 exposed by fenestration on both sides, Queensland (figd. Owen, 1874, pl. 77, figs. 2-6; 1877, pl. 90, figs. 2-6; Stirton and Marcus, 1966, figs. 1a-b).

F3866, cast of holotype *Pachysiagon otuel*, B.M.(N.H.) specimen, 46310, partial right mandibular ramus with M_2–M_4, King Creek, Clifton, Darling Downs (figd. Owen, 1874, pl. 76, figs. 7-10; 1877, pl. 89, figs. 7-10; Stirton and Marcus, 1966, fig. 6).

F810, partial right maxilla with P^2–M^2, P^3 removed by fenestration, Darling Downs. F2987, partial right maxilla with P^3–M^4, Darling Downs (figd. in part, De Vis, 1895, pl. 16, figs. 3-4). F2988, partial left maxilla with M^2–M^4, Darling Downs, possibly from same individual as F2987. F2989, partial left maxilla with P^3–M^3, Condamine River, "Armour", Macalister, Darling Downs. F4471, partial right maxilla with M^1–M^2, Darling Downs.

F806, associated partial mandibular rami with right M_1–M_4, left M_1–M_4, Darling Downs. F808, partial right mandibular ramus with P_3–M_3, Darling Downs (figd. in part De Vis, 1895, pl. 16, figs. 1-2). F2979, partial right mandibular ramus with M_2–M_4, Gowrie, Darling Downs. F2981, partial right mandibular ramus with P_3 broken, M_1–M_4, ? Gowrie. F2982, associated partial mandibular rami with right P_3, M_1–M_4, left P_3, M_1–M_4, Clifton, Darling Downs. F2983, partial left mandibular ramus with M_1, M_3 in its crypt, Darling Downs. F2984, partial right mandibular ramus with P_3 and M_4 erupting, M_1–M_2, Darling Downs. F2985, partial right mandibular ramus with M_2–M_4, ? Pilton, Darling Downs. F2986, partial left mandibular ramus with M_2–M_3, Darling Downs. F4472, partial right mandibular ramus with M_2, Darling Downs. F4470, partial left mandibular ramus with M_2–M_3, Darling Downs. F4469, partial left mandibular ramus with M_2, Darling Downs. F4468, associated partial mandibular rami with right I_1, P_3–M_4, left I_1, P_3–M_1, King Creek, between Nobby and Pilton, at M.R. 039454 Clifton 1 mile sheet, Darling Downs. F4467, near complete associated mandibular rami with right I_1, P_3–M_4, left I_1, P_3–M_4, King Creek, between Nobby and Pilton, at M.R. 039454 Clifton 1 mile sheet.

SPECIFIC DIAGNOSIS: An adequate diagnosis for the species is presented in Stirton and Marcus (1966).

DESCRIPTION: Upper incisors are not preserved in any specimen. P^2 is too fractured to permit a description to be made, while DP^3, although molariform, is broken anteriorly in the only specimen containing the tooth. The posterior loph indicates that the tooth probably had similar structure to the molar series.

P^3 comparatively robust, elongate, but shorter than M^1, broader posteriorly than anteriorly. Longitudinal labial crest high, well defined, continuing to ascend posteriorly from metacone towards base of crown in most specimens, but occasionally without posterior extension; anterior extension from paracone less well defined, often absent; crest transected by two sets of vertical labial and lingual ridges between cusps. Postero-labially, strong ridge frequently descends towards metacone but only rarely is well defined postero-labial fossette developed. Strong ridge ascends lingually from paracone to protocone as does well defined ridge from metacone to hypocone; anterior and posterior ridges ascending from hypocone and protocone respectively constitute relatively low lingual cingulum; cingulum slightly concave lingually in occlusal view, not significantly marked by cuspules in lateral view. Posterior ridge from hypocone curves labially to below metacone delimiting low postero-lingual fossette. Lingual basin relatively shallow,

variably ornamented by moderately strong accessory ridges between base of longitudinal crest and lingual cingulum. Anterior ridge from protocone rarely developed and then weak; antero-lingually, crown occasionally slightly excavated and plicate.

TABLE 6

MEASUREMENTS FOR *Procoptodon pusio* OWEN MAXILLAE

Specimen	P^2	DP^3	P^3	M^1	M^2	M^3	M^4
F3863 cast	—	*12.8 × 11.4	11.9 × —	*13.9 × 13.4	16.8 × 14.8	18.3 × 15.3	—
of holotype	—	*13.0 × 11.6	12.3 × 10.1	*13.6 × 13.4	16.2 × 15.3	18.0 × 16.0	—
F810 ..	8.7 × —	10.3 × —	—	12.7 × —	14.5 × 13.2	—	—
F2987 ..	—	—	12.9 × 9.4	13.1 × 13.0	15.6 × 14.3	17.9 × 15.5	18.4 × 15.0
F2988 ..	—	—	—	—	15.5 × 14.2	17.9 × 15.0	18.4 × —
F2989 ..	—	—	11.9 × 8.3	13.1 × 12.3	15.8 × 14.6	18.1 × 16.0	—

*Measured from Owen (1874, pl. 77, figs. 2-6).

$M^1<M^2<M^3<M^4$; molars subrectangular, slightly constricted across median valley, with lophs moderately high, somewhat bowed anteriorly; metaloph broader than protoloph in M^1, approximately equal in M^2, and narrower in M^3 and M^4. Lateral loph surfaces converging only slightly ventrally. Anterior cingulum relatively narrow, only very slightly ascending lingually, short; labial margin of cingulum connected to paracone by well defined ridge; moderately few ridges ornament anterior surface of protoloph and of these only one or occasionally two low ridges cross to the cingulum; no well-defined forelink present; occasionally, low tubercular ridge passes above cingulum from labial margin to about mid-line of crown. Median valley sharply U-shaped, but sometimes V-shaped particularly in anterior molars, slightly ascending lingually. Strong midlink ascends from point labiad to mid-point of protoloph, to unite with ridge from below mid-point of metaloph, above median valley; midlink usually sinuous in occlusal view, but generally convex labially, ornamented labially and lingually by variable weak, vertical ridges. Relatively strong ridge ascends posteriorly from point linguad to mid-point of protoloph, subparallel to midlink, uniting with posterior loph surface towards base, or with side of midlink. A second, moderately strong ridge ascends postero-lingually from paracone, uniting with short ridge from midlink to delimit well defined fossette on postero-labial protoloph surface; rare, very weak ridge descends posteriorly from this towards median valley. Slight ridge from protocone ascends postero-labially on posterior protoloph surface. Anterior ridge from metacone weak, ascending antero-lingually towards median valley without production of antero-labial fossette on anterior metaloph surface; anterior hypocone ridge very weak. Anterior metaloph surface rarely ornamented by additional accessory ridging. Base of

median valley near planar, without development of marked pockets. Posterior metaloph surface with strong ridge ascending almost directly lingually from metacone while broader, posterior ridge ascends labiad to this; second strong ridge ascends from point about one quarter distance along metaloph crest from hypocone, curving abruptly labially near crown base to unite with lingual metacone ridge; weaker ridge from hypocone subparallel to this. Posterior fossette present above mid-line of crown. Moderately strong ridge ascends from near mid-point of metaloph crest into posterior fossette. Coarsest ridges throughout crown, occasionally ornamented by extremely weak subsidiary ridging.

Mandible strong, comparatively large, deep, with longitudinal axis slightly convex laterally. Symphysis relatively elongate, ankylosed in adult specimens, set at an angle of approximately 40° to base of mandible; produced postero-ventrally resulting in marked ventral extension of basal margin of ramus below P_3–M_1; geniohyal pit very deep, set high and well anterior to posterior symphyseal limit. Diastema short; ventral margin of ramus acutely rounded between symphysis and diagastric ridge. Mental foramen large, ovate, ventral and only slightly anterior to anterior root of P_3, below diastemal crest; accessory foramen absent. Ramus with labial groove moderately well defined, developed from between mental foramen and P_3 to below anterior roots of M_3, close to alveolar margin. Diagastric process strongly developed separated from base of angle by post-diagastric sulcus, bounded above by diagastric fossa; this fossa separated antero-dorsally from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf moderately short, leading to post-alveolar ridge, ascending posteriorly on mesial wall of large coronoid process, to above relatively large mandibular foramen. Masseteric crest raised to about level of occlusion of cheek teeth, with production of very deep, masseteric foramen and deep masseteric fossa. Anterior margin of coronoid process inclined almost 20° beyond vertical. Angle of mandible markedly inflected. Condyle not preserved in any specimen.

I_1, relatively small, weak, with crown curved dorsally and mesially to approximate with incisor from other ramus; antero-ventral surface markedly curved. Crown and root laterally compressed, with crown subovate in section, tapering somewhat distally. Young individuals with tips passing posterior to I^1, but older individuals showing anterior wear facet with I^1. Dorsal enamel flange with wear facet near planar.

P_2 and DP_3 are not retained in any specimen.

P_3 relatively large, but smaller than M_1, subovate to subtriangular in occlusal view, broader posteriorly. Crown with high lingual crest very slightly concave lingually, transected between cuspids by two and occasionally three sets of vertical labial and lingual ridges, with production of cuspules at crest. High, curving, labial crest separated from posterior continuation of lingual crest by vertical groove; anteriorly, labial crest unites with first cuspule along lingual crest from anterior cuspid. Labial ridge from anterior

cuspid curves posteriorly to unite with labial crest below dorsal limit of crown. Slight cuspule frequently present at anterior base of crown. Basin between crests variably presents accessory ridging.

TABLE 7

SUMMARY OF MEASUREMENTS FOR *Procoptodon pusio* OWEN MANDIBLE

Character	F3866, cast of holotype *P. otuel*	n	O.R.	$\bar{X}$	s	V
Length P_3	—	6	9.7 — 10.2	9.9	0.1897	1.92
Maximum breadth P_3 ..	—	6	6.0 — 6.4	6.3	0.1673	2.66
Length M_1	—	7	12.5 — 13.4	12.9	0.3391	2.63
Breadth protolophid M_1 ..	—	6	9.4 — 10.2	9.9	0.3134	3.17
Length M_2	16.0	16	12.7 — 16.5	14.9	0.9699	6.51
Breadth protolophid M_2 ..	—	8	10.9 — 12.1	11.6	0.4017	3.46
Length M_3	17.1	13	15.9 — 18.0	16.6	0.6799	4.10
Breadth protolophid M_3 ..	12.0	12	12.0 — 13.6	12.7	0.5300	4.17
Length M_4	18.4	12	16.8 — 20.0	18.1	0.7316	4.04
Breadth protolophid M_4 ..	11.5	11	11.5 — 13.7	12.6	0.6253	4.96

$M_1<M_2<M_3<M_4$; molars subrectangular in occlusal view, slightly to moderately constricted across talonid basin; lophids moderately high, slightly convex posteriorly, with lateral lophid surfaces converging only slightly dorsally. Hypolophid broader than protolophid in M_1, approximately equal in M_2, equal or slightly narrower in M_3, and narrower in M_4. Trigonid basin relatively broad, its length approximately equalling distance between lophids. Forelink high, strong, sharply curving anteriorly to appear markedly concave labially in occlusal view; forelink descends to point well labiad to mid-line of crown; high transverse ridge unites with forelink well above anterior cingulum, extending from above antero-labial margin to lingual cingular limit; strong ridge descends anteriorly from protoconid into talonid, but anterior metaconid ridge very weak. Trigonid basin with well defined antero-labial fossette. Accessory ridges on anterior surface of protolophid, forelink and transverse ridge variable but usually weak and numerically few in number. Posterior surface of protolophid usually unornamented, and where present, accessory ridging very weak. Midlink descends antero-lingually from hypoconid, then strongly curves anteriorly to unite with short ridge from point labiad to mid-point of protolophid; junction rarely marked by more than vertical grooves, accessory ridges from midlink usually transverse but moderately weak, and most are developed lingually. Anterior ridges from hypoconid and entoconid weak; accessory ridges on anterior surface of hypolophid variable but usually weak and numerically poorly represented; lingually, that closest to midlink usually somewhat better developed. Talonid basin sharply U-shaped,

near planar transversely. Posterior surface of hypolophid rounded, usually with broad basal ridge extending dorsally; ridges from hypoconid and entoconid generally weak, but that from entoconid usually the stronger of the two; posterior surface of crown variably ornamented by weak vertical ridges. All ridges and accessory ridges throughout generally less well defined than in other species.

DISCUSSION: As with *Procoptodon rapha*, redescribed above, the name *P. pusio* was introduced in abstract by Owen (1873) as a *nomen nudum*, but was published, accompanied by an adequate description and figure in a subsequent study (Owen, 1874). The holotype is well preserved, and being juvenile, shows little evidence of occlusal wear in permanent erupted cheek teeth. P^3 has been exposed by fenestration to indicate the morphological characters of that tooth.

The type locality is not mentioned in Owen (1874) but is listed by Lydekker (1887) as Queensland. It is highly likely that it was derived from the Pleistocene fluviatile deposits of the Darling Downs. The specimen was donated by Sir D. Cooper, and where specified, most material emanating from this source came from the eastern Darling Downs, particularly from Gowrie.

In early publications, the lower dentition of this species was referred by Owen (1873, 1874) to a separate genus and species, *Pachysiagon otuel*. Although this name had page precedence over *P. pusio*, Owen (1877) as first revisor, recognised *P. pusio* as the valid name for the taxon, and placed *P. otuel* in synonymy. Owen's action is supported by the present study, in contrast to the conclusion reached by Lydekker (1887) who retained *Procoptodon otuel* as a valid taxon, but placed *P. pusio* in synonymy with *P. rapha*. This is not upheld when a size comparison is made, nor can it be justified by consideration of morphology, as both mandibular and maxillary cheek teeth present reduced ornamentation compared with *P. goliah* and *P. rapha*. De Vis (1895) reverted to the use of the specific name "*otuel*" for the taxon, but Stirton and Marcus (1966) have correctly reapplied the name *P. pusio*. These authors have indicated the type locality for *P. pusio* as King Creek, Darling Downs. This locality, in fact, belongs to the holotype of *Pachysiagon otuel* and not to the holotype for *P. pusio*.

De Vis (1895) considered *P. goliah* and *P. rapha* synonymous, and that "mean size" was no reason for the separation of *P. pusio* from this group. He considered, however, that the difference between the largest widths in *P. goliah* and the smallest in *P. pusio* precluded this possibility and rendered their identity impossible.

Upper dentition in the present sample is too poorly represented to allow meaningful statistical treatment. Morphologically, the sample indicates similar structural simplicity to the holotype, compared with the larger species, *P. goliah* and *P. rapha*. This is parti-

cularly evident in the reduced accessory ridging. The structure of P^3 is, however, somewhat different in those specimens possessing it. In F2987, a well defined postero-labial fossette is present near the metacone, while in F2989, the lingual basin is marked by a strong ridge, subparallel to the longitudinal crest in the posterior portion. In no cases are the differences as great as between the holotype P^3 and those of the larger species.

The mandibular specimens are very similar morphologically to the holotype of *Pachysiagon otuel* and form a sample sufficiently large to permit statistical analysis. A summary of mandibular measurements is provided in table 7. The unity of the material is indicated by the relatively low values for the Coefficient of Variation throughout. In most instances V has a value well within that expected for a sample from a single population from slightly differing stratigraphic levels (Simpson et. al., 1960). In the case of length of P_3 this value is low, presumably because of small sample size. The value for length of M_2 is slightly higher than is normally expected, and as the sample is adequate, this may represent greater than normal variability in this feature.

As with the upper cheek teeth, structural simplicity is generally the rule, although occasional specimens, as with F808, show somewhat more complex accessory structure. Structural similarity and size indicate the correct association of upper and lower remains, although these have not, as yet been referred to the species.

REMARKS

At present, three species of *Procoptodon* Owen are known from Upper Cainozoic deposits in Australia, these comprising the large *P. goliah*, the slightly smaller *P. rapha* and the much smaller *P. pusio*. The species are moderately widely spread, particularly the larger forms, but are known from relatively few localities, and are at present known only from the eastern portion of the continent and possibly Tasmania. All are restricted to sediments believed to be of Pleistocene age.

Figure 1 presents information on some of the data derived from the Darling Downs populations of the three species in the form of a log difference diagram (Simpson, 1941), showing comparatively, the proportional relationships of some mandibular dental parameters. It is apparent that although *P. rapha* is relatively and actually smaller than *P. goliah* in most characters, its P_3 is relatively longer. Both *P. pusio* and *P. rapha* have posterior lower molars which become progressively smaller than those in *P. goliah*. Some indication of the position relating to upper cheek teeth is also presented in figure 2, but in this the comparison is rendered less valuable by the small samples involved. To a limited extent, conclusions drawn from lower molars are true of molars in *P. rapha*, but in *P. pusio*, a larger sample, the comparison between upper and lower molars is not paralleled to the same extent.

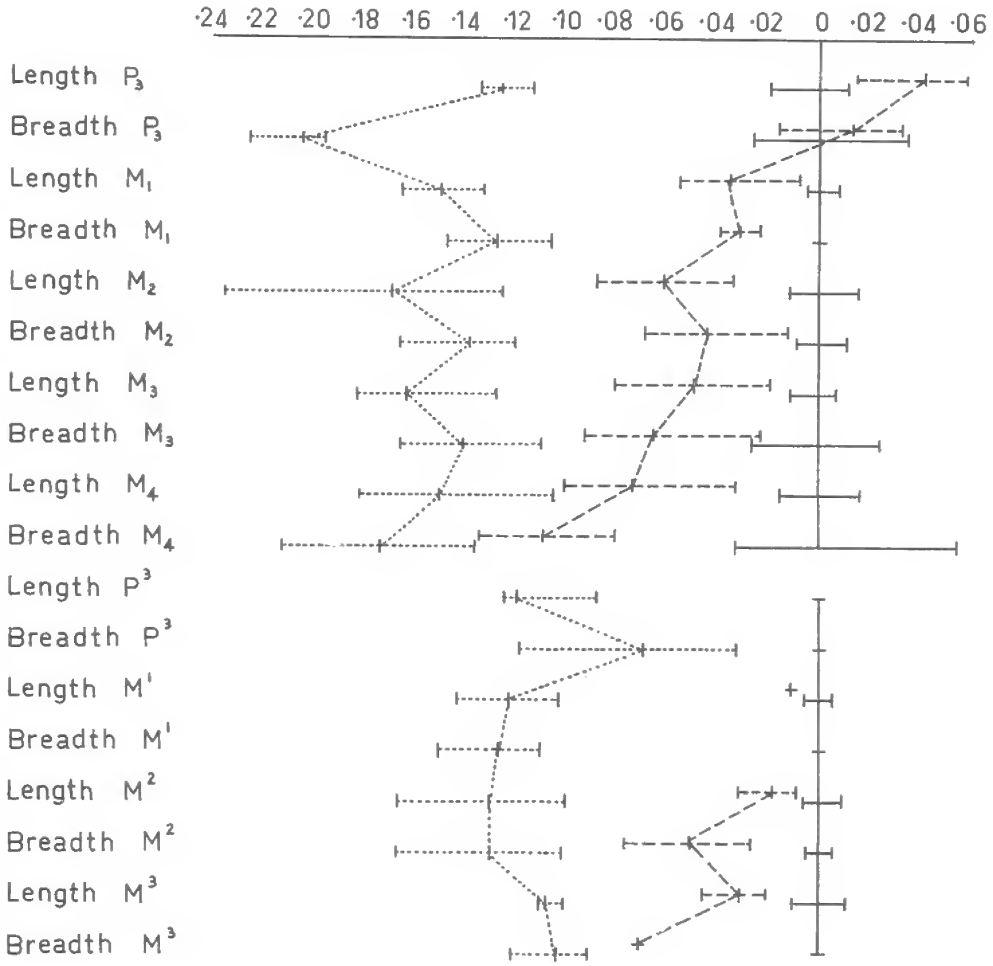

FIG. 1: Log Difference Diagram indicating the proportional relationships of samples of lower and upper permanent cheek teeth in *Procoptodon rapha* and *P. pusio*, utilising data for the mean of the *P. goliah* sample as standard. Coarse dashes represent *P. rapha*; fine dashes represent *P. pusio*. Horizontal limits are based on observed ranges while mean values have been included and have been joined to facilitate comparison.

Ride (1959) has presented observations of masticatory adaptations as they relate to *Procoptodon*. While his comments are valid for the mandibular remains considered, the inclusion of possible phylogenetic implications relating to the premaxillary dentition have been shown by Tedford (1966) to be inappropriate, the specimen in question actually being of a species of *Sthenurus*, most probably *S.* (*Simosthenurus*) *orientalis*.

On the basis of cranial and dental morphology alone it is apparent that the genera *Sthenurus* and *Procoptodon* are closely related. The geological record indicates the group

had its origin in the late Tertiary. *Sthenurus* is well established and diverse in the Chinchilla Sand (Bartholomai, 1963), while Woodburne (1967) has shown the presence of a possibly related form, *Hadronomas puckridgi* in the Alcoota Fauna of the late Miocene or early Pliocene Waite Formation of central Australia. *H. puckridgi*, however, also presents features observable in grazing macropodids, and the permanent premolars are very similar to those in the protemnodonts. As indicated by Tedford (1966) there is little reason to doubt the derivation of the larger browsing forms from more generalised macropodines. However, as shown above there is no evidence to support a considerable antiquity for the *Sthenurus–Procoptodon* group, based on their browsing adaptations, as suggested by Tedford (1966). The earliest record of the group from the Lake Eyre Basin is of an isolated incisor of Pliocene age (Stirton et al., 1961).

Tedford's (1966) suggestion of parallel evolutionary trends of *Procoptodon* and the brachycephalic *Simosthenurus* during the Pleistocene appears reasonable, although there is no supporting evidence to suggest that his contention of a dichotomy before the Pliocene is correct. It is felt that on the basis of current evidence this took place no earlier than the late Pliocene or even early Pleistocene and that adaptive radiation in the group as a whole has been rapid.

The current study is based solely on cranial specimens and no attempt has been made to associate post-cranial specimens. All specimens, with the exception of one partial mandible from fissure-fill deposits, have the appearance of derivation from fluviatile sedimentary deposits. Prospects for locating articulated skeletons in such deposits are limited because of the scattering of elements which generally takes place prior to burial.

Procoptodon, in its aberrant structural characters and extreme specialisation, constitutes one of the most interesting of the macropodine genera. It evolved to the stage where its browsing habits must have dominated its way of life. This trend was much more complete than in short-jawed species of *Sthenurus* which were also adapted for a similar habitat.

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